Leigh Jr.
Evolution: Education and Outreach (2022) 15:7
https://doi.org/10.1186/s12052-022-00165-3

Evolution: Education and Outreach

REVIEW

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How predictable is evolution in a chancy world where evolution's raw material is random mutation?

Egbert Giles Leigh Jr.*

Abstract

This is a review of *A Series of Fortunate Events*, by Sean B. Carroll. First, Carroll uses the decisive role of chance in our lives to deny validity to anthropocentric religion. Then he discusses impacts of chance environmental disasters on the course of evolution, the random origin of all variation on which natural selection acts, and the decisive role of chance in human lives.

Keywords: Anthropocentrism vs objective science, Biotic crises and evolution, Chance in evolutionary outcomes, Chance in human lives, Evolutionary convergence, Major evolutionary innovations, Monod, Jacques, Natural selection, Predictability of evolution

Book details

Title:	A Series of Fortunate Events,
H/b ISBN:	978-0-691-20175-7,
Price:	$22.95,
Number of pages:	Pp. viii + 214,
Written by:	Sean B. Carroll,
Published by:	Princeton University Press, Princeton, NJ in 2020.

Book review

Sean Carroll is a skilful and prolific writer. He made major contributions to developmental biology (Carroll 2005) that helped answer the question of Behe (1996) whether random mutation could fuel adaptive evolution. He also explains biology clearly to the general public: a major achievement is his immensely successful book, *The Serengeti Rules*, on regulatory mechanisms in biochemistry, physiology and ecology (Carroll 2016).

In *A Series of Fortunate Events*, Carroll argues that evolution, like individual human lives, largely reflects the effects of chance. Like Monod (1972) in *Chance and Necessity*, Carroll thinks this decisive role of chance implicitly falsifies anthropocentric religions such as Christianity. This contrasts with previous views: three centuries ago, Pascal complained that the determinism of Descartes's mechanical world left no place for God's action once He gave "the flick of the fingers, to set the world in motion" (Pascal 1976, Pensée 77). This determinism, emphasized by Laplace, was characteristic of physics until the advent of quantum mechanics and chaos theory (Prigogine 1997). Carroll's argument, and his predecessor's, raise two major scientific issues. First, did Monod's view of objectivity, designed to strip science of anthropocentrism, lead him to overrate the role of chance in life's origin? Second, given the random origin of the variation natural selection acts on, and the importance of chance events in evolutionary history, what, if anything, can we predict about the forms of life that will evolve?

*Correspondence: bufotyphonius@gmail.com
Baltimore, MD, USA

On p. 6 Carroll first states the project he intends for his book: to further confound anthropocentrism by updating in the light of recent research the argument of Monod (1972) that evolution is the product of chance. His project's first step is recounting a particularly improbable but devastating event: the collision, 65 million years ago, of a bolide 10 km wide with Mexico's Yucatan, creating the >160-km-wide Chicxulub crater and triggering a series of worldwide catastrophes (p. 31: see also Schulte et al. 2010). This collision extinguished the dinosaurs (excepting a few birds) and this chance event opened the way for larger mammals to diversify and human beings to evolve. He then remarks on the ability of human beings and their ancestors to survive the world's cooling when India collided with Asia over forty million years ago, raising up the Himalaya and the Tibetan plateau (pp. 43–46), and later disruptive climate shifts. Notable among these shifts were the glaciations and the briefer, more frequent, often ferocious climate changes in the Pleistocene (pp. 46–52).

After mentioning the improbable series of events that led Darwin to form his theory of evolution by natural selection, Carroll introduces his second major theme: the random origin of the variation selection acts on. He first remarks (p. 79) that Darwin considered that this variation arose as products of accident. Then he updates the argument of Monod (1972, pp. 112–115) that mutations, like typographical errors, are random in both when they occur and the lack of relationship between their effects and the organism's, or manuscript's, needs. Carroll shows in detail how a quantum jump can cause a guanine-cytosine couplet in a DNA sequence to be copied as an adenine-thymine couplet (p. 93). He compares (p. 91) bacterial DNA replication, which can copy 60,000 bases per minute, with less than one error per 10,000 bases, with the average professional human typist, who copies 300 characters per minute, with one error per 30 characters. Of course, in both cases, first drafts are proofread: bacterial proofreading mechanisms reduce the final error rate to less than one per billion bases. Bacteria can control mutation rate, but not the effects of mutation.

Carroll now asks (p. 100) the century-old question: which is the creative factor in evolution: natural selection, as Darwin thought, or mutation, the opinion Carroll ascribes to Monod? Monod (1972: 112–113) did say that mutations, the only possible sources of genetic innovation, are random events, so "chance alone is the source of every innovation, of all creation in the biosphere." Carroll mentions cases where one or two mutations had a decisive influence. One is the mutation that programmed crests of feathers on a pigeon's head (pp. 100–108), which led pigeon fanciers to develop several breeds of crested pigeons by artificial selection. Another is the two mutations that jointly enabled a Siberian woolly mammoth's hemoglobin to release oxygen in its cool extremities (pp. 109–111), one of the several adaptations that allowed the ancestors of woolly mammoths to invade wintry settings. Natural selection can indeed do nothing without those random mutations.

Natural selection, however, sifts the few beneficial mutations from the countless multitude of harmful ones. Multicellular organisms have features that facilitate such sifting: sexual reproduction and recombination (McDonald et al. 2016; Leigh and Ziegler 2019). Fair meiosis ensures that selection favors only mutations that benefit the organisms carrying them (Leigh 2010, p. 10, Scott and West 2019).

Monod (1972, pp. 23–24) also remarked that the initial appearance, spread by selection and steady refinement of ever better adapted characteristics, are due to mutations in a structure possessing the property of invariance, in the form of nearly precise replication, that can preserve the effects of chance replication errors and thereby submit them to the play of natural selection. After all, thanks to the genome's faithful replication, one beneficial mutation's spread allows the occurrence and spread of a second mutation amplifying the first's effect, and so onward, until the adaptation initiated by the first mutation is perfected (pp. 116–118, Weinrich et al. 2006). More generally, mutation provides the elements from which natural selection confects, step by step, organisms adapted to their roles in their ecosystem, just as pigeon fanciers select for those new features that together yield a breed of pigeons of pleasing or fascinating appearance (pp. 100–107). Thus natural selection is the organizer and coordinator that confers order and adaptation on living beings. Carroll (p. 120) is misled when he views "all the beauty, complexity and variety of life" and concludes that "We live in a world of mistakes, governed by chance."

The part of the book bearing on the scientific issues Carroll raises ends on p. 122. In the rest of the book he strives to "make chance personal" (p. 125) by exploring its role in individual human lives. He explains luminously why each human being's genotype (barring identical twins) is unique (pp. 130–134) and remarks that 1% of babies have a disorder determined by a new mutation, and 5% will suffer some genetically determined disorder (pp. 134–135). He discusses in detail a male homosexual homozygous for a mutant that altered his white blood cells in a way that the AIDS virus could not enter them and destroy his immune system (pp. 136–144). Then he discusses the role of chance in when and how we die. He gives a fascinating account of how chance somatic mutations cause often fatal cancers, and why the probability of most but not all cancers increases sharply with old age (pp. 152–162). He ends the book (pp. 163–168) with a most remarkable conversation he constructs from published quotes and what he heard the others say, involving himself, Monod, the authors Camus and Vonnegut, and six comedians, concerning the role of chance in their lives.

Carroll has raised two scientific questions. First, how probable was life in our universe? Monod (1972, p. 21) rightly asserts that the cornerstone of the scientific method involves systematically denying that phenomena can be validly explained in terms of "final causes" (even though Aristotle's foundation of biology involved the free use of final causes: Leroi 2014). This principle leads Monod (1972, p. 145) to argue that "The universe was not pregnant with life." On this earth, however, if vents where alkaline fluids replete with H_2 and other elements welling up from below the sea surface met acidic ocean water replete with CO_2 in a foam of bacterium-sized cells with semipermeable membranes of FeS were already present four billion years ago, the appearance of life was probably inevitable (Lane 2009, 2015). To generate a planet like earth, however, the universe had to be long-lived, truly gigantic, and capable of generating long-lived stars. These requirements impose very restrictive conditions on the fundamental constants of nature (Smolin 1992, 1997). Smolin would like to understand why these constants have such strange values. Conway Morris (2003, pp. 69–105) argues that even in this universe an extraordinary concatenation of circumstances is required to yield a planet as propitious as earth for the origin of life.

The second question is: given that natural selection, acting on chance modifications of already adapted phenotypes, is the source of the adaptation and diversity of living beings (Monod 1972, pp. 118–119), how much can we predict about the products of evolution? Conway Morris (2003, p. xi) suggests that most evolutionary biologists would agree "that the likelihood that 'exactly the same cognitive creatures—with five fingers on each hand, a vermiform appendix, thirty-two teeth and so on' evolving again if, somehow, the Cambrian explosion could be rerun is unlikely in the extreme." Can we predict more general features of the products of evolution? If so, how could we do it?

The approach of Vermeij (2006) is to ask if most innovations leading to significant diversification, from the origin of life onward, occurred repeatedly. If most such innovations occur only once, independent origins of life would generate very different histories. If most innovations are repeated, even if only one lineage survives, then evolutionary "histories would be replicable at the level of functional roles and directions of adaptive change" (Vermeij 2006, p. 1804). Vermeij (2006) argues that, especially before the Cambrian, the fossil record is too incomplete and difficult to interpret to decide whether or not most innovations were repeated. In the last three hundred million years, when the fossil record is more complete and more interpretable, most such innovations did occur repeatedly: he therefore infers that the same was also true beforehand.

Monod (1972, p. 126) remarked that "if terrestrial vertebrates appeared and were able to initiate that wonderful line from which reptiles, birds and mammals later developed, it was originally because a primitive fish 'chose' to do some exploration on land." Similarly, eusociality began evolving in nocturnal bees, *Megalopta*, when some female "chose" to "domesticate" a daughter or two as non-reproductive workers (Kapheim et al. 2020). Monod thought that, especially in higher animals, behavior leads evolution by "orienting the pressure of selection," a thesis most recently evaluated by Wcislo (2021). This process is reinforced by the environmentally responsive flexibility of development (West-Eberhard 2003). Given the repeatability of morphological innovations, including those favored by behavior, might not the influence of behavior enhance evolution's predictability?

Conway Morris (2003) assessed the predictability of evolution from the degree of morphological and physiological convergence among different organisms independently adapting to similar challenges. Such convergences include some Gnetales, which like some flowering plants, evolved 'double fertilization,' visual attraction of animal pollinators by "flowers," and xylem vessels and leaf venation similar to flowering plants (Conway Morris 2003, pp. 136–137). Similarly, ichthyosaurs evolved streamlined shapes, smooth skin, homeothermy, and insulating blubber, similar to the dolphins which evolved much later (Lindgren et al. 2018). Finally, Madagascar has evolved a genus of brightly colored forest floor frogs, *Mantella*, greatly resembling in color and habits the poison-dart frogs (Dendrobatidae) of tropical American forest floors, In both *Mantella* and the dendrobatids, the bright colors warn of (remarkably similar) poisons in their skins, sequestered from some of the arthropods they eat (Clark et al. 2005; Conway Morris 2003) provides enough examples of evolutionary convergence to lend force to the idea that the major features of evolution are predictable.

Life came into being with the 'invention' of a replicable structure storing information that enabled this structure's bearers to acquire enough energy, and deploy it appropriately enough, to survive and reproduce (Lorenz 1977, p. 171). How this energy can be acquired, defended and deployed is constrained by the laws of physics and chemistry. These constraints may so limit options for practicing particular ways of life that evolution becomes predictable. Conway Morris (2003, p. 146) remarks, and provides evidence, that under extreme conditions feasible options for coping are most restricted and evolutionary convergence most likely. McNab (2012) explores some of these constraints.

Finally, evolution is ruled by the competitive process of natural selection. A new phenotype benefits from avoiding competition by occupying new habitats or exploiting unused resources. Thus, once primary producers evolve, consumers of their wastes, decomposers of the dead, and predators of the living will appear. Some of these ways of life call forth selection for new sensory capacities and modes of locomotion. New habitats will be colonized. A soil-forming community of prokaryotes appeared on land three billion years ago (Retallack et al. 2016), followed by many subsequent colonizations. Once eukaryotes evolved, forcing the evolution of orderly sexual reproduction (Lane 2015, pp. 211–215) and enabling a better distribution of energy within cells and larger genomes, complex multicellular organisms evolved thrice, and eusocial animals evolved many times, each step enabling new ways to make livings. Cooperative groups evolve, however, only if cheating (benefiting from the work of fellow group members without contributing to these benefits) can be sufficiently restricted. This can happen by two standard routes: forming groups of close relatives, so one spreads one's own genes by helping others, or cooperating to cope with a common threat so strong that all must cooperate to survive (Leigh 2010; Leigh and Ziegler 2019). Cooperative groups can be transformed into coherent individuals, as in the evolution of complex multicellular organisms (a major evolutionary transition: Maynard Smith and Szathmáry 1995) only if all conflicts of interest can be annihilated. There are only a few ways to achieve this (Leigh 1991; Leigh and Ziegler 2019). The role of natural selection in driving adaptation therefore enables us to predict many features of evolution.

This book is clearly written. Its examples are well chosen, clearly explained, and telling. They are also instructive in their own right. The imagined conversation between comedians, two philosophical novelists, and two molecular biologists is well worth reading. Nevertheless, Carroll underrates the creative power of natural selection, and the implications of evolutionary convergence and the repeated occurrence of most diversity-triggering evolutionary innovations. He therefore underrates how much we can predict about the "products" of evolution.

Acknowledgements
The author is most grateful to E. Allen Herre for constructive criticisms and to Revati Gireesh for her guidance through the process of electronic submission.

Author contributions
EGL read the book and wrote the book review. The author read and approved the final manuscript.

Funding
The author received no funding for preparing this book review.

Availability of data and materials
Not applicable.

Declarations

Competing interests
The author declares that he has no competing interests.

Received: 23 February 2022 Accepted: 4 April 2022
Published online: 04 May 2022

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